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OYSTER REEF AS HABITAT FOR ESTUARINE MACROFAUNA



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**OYSTER REEF AS HABITAT FOR
ESTUARINE MACROFAUNA**

BY

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ABSTRACT

We assessed an oyster reef as nursery habitat for juveniles of economically important penaeid shrimps, blue crab, stone crab and game fishes. This is the first investigation to compare densities of fauna on an oyster reef with those in salt marsh and bare mud habitats. The study used drop trap sampling methodology in West Bay, Texas, during December of 1988 and July of 1989.

Oyster reef and salt marsh habitats were each used by comparatively large numbers of fishes and decapod crustaceans, but species composition between the habitats differed considerably. These differences were particularly apparent among species of direct economic importance. For instance, juveniles of brown shrimp, white shrimp, blue crab, and spotted seatrout were significantly less abundant on the oyster reef than in either the marsh or mud habitats. Juvenile stone crabs, by contrast, were significantly more abundant on the oyster reef. Small forage animals, including bait fishes, and infaunal and epifaunal worms and crustaceans, which serve as prey for juveniles of economically important species, were also abundant on the reef and in the marsh. But, like the larger fauna, species composition differed.

The structured habitats (reef and marsh) generally had significantly higher numbers of fauna than bare mud habitat. Nonetheless, there were seasonal differences. During the winter, when faunal densities were low, juvenile penaeid shrimps and blue crabs were significantly more abundant on the mud bottom than either the reef or the marsh, attributable to the effect of low winter tides. Since the oyster reef and salt marsh are both intertidal, periods of extended low water (as normally occurs in the winter) greatly limits the availability of these habitats. Consequently, utilization of subtidal mud bottom expands during the winter. Also, since all habitats are not equally available in the winter, winter distributions do not necessarily reflect habitat selection (preference). During the summer, long periods of high water offered greater opportunity for habitat selection by natant fauna. Therefore, the high abundances

of penaeid shrimps, spotted seatrout and blue crab in the salt marsh compared to oyster reef and subtidal mud bottom, during the summer, appears to reflect authentic habitat selection. Since juvenile stone crabs only occurred on the oyster reef, in both the winter and summer, the intense selectivity by this species for reef habitat was revealed.

INTRODUCTION

Background

A great deal of information exists on the biology and ecology of oysters themselves (see reviews by Butler 1954; Galtstoft 1964; Bahr and Lanier 1981; Burrell 1986), but very little is known of the value of oyster reefs as habitat for exploiting estuarine species. This is especially apparent in comparing oyster reefs with other estuarine habitats such as salt marshes, seagrasses, bare sand or mud flats, and rock reefs. Nonetheless, previous investigations (Wells 1961; Bahr 1974; Dame 1979) have indicated high diversity and abundances in faunal associations with oysters. Large numbers of annelid worms and small crustaceans, present as epifauna and infauna, that might be used as food by larger consumers have been reported in the literature. Still, information on utilization of reefs by mobile secondary consumers remains incomplete. Important questions such as whether penaeid shrimps or juveniles of other economically important species use reefs as nursery habitat for protection or feeding are yet unanswered. Community structure and trophic relationships in oyster reef communities are only partially defined. Comparison of oyster reef habitat functions with other habitats, and relationships of fauna associated with oyster reefs to fauna associated with other estuarine habitats are not clear. In the following study, we address the question of nursery value of oyster reefs.

Purpose

The purpose of the investigation was to establish the relative value of an oyster reef as

nursery habitat for exploiting natant estuarine species. This was accomplished by comparing densities of fishes and decapod crustaceans on an oyster reef to faunal densities in a *Spartina alterniflora* salt marsh and on nonvegetated subtidal mud bottom. The working hypothesis is that animal abundances on an oyster reef are similar to those of habitats with complex physical structure, such as a salt marsh surface, and dissimilar from those without complex physical structure, such as barren mud bottom.

As far as we are aware, this is the first study of its kind. The data and analyses are informative but also must be considered preliminary. The results are from two surveys in one bay, one taken during the winter (cold season) and the other taken in the summer (warm season). As expected in a preliminary study, many interesting, relevant questions have been raised. Most of the questions are readily addressable, given new methods at our disposal, and they should be pursued in continuing investigations.

METHODS

Study Sites

The study was conducted in West Bay, Texas, a shallow body of water formed behind Galveston Island. This is a mesohaline to euhaline bay near the coast in the greater Galveston Bay system. Water exchange with the Gulf of Mexico is through San Luis Pass and Bolivar Roads Channel, two tidal passes situated at either end of Galveston Island. Oyster reef, salt marsh and subtidal bare mud bottom are prominent habitats in the bay. For this study, sites of each habitat type were selected within 4 km of each other. The oyster reef site was at Confederate Reef in the eastern end of the bay. The salt marsh site and subtidal bare mud site were both located along the shoreline of Galveston Island State Park, in about the middle of the bay.

Field Procedures

Drop trap sampling, described by Zimmerman et al. (1984), was used in the study to quantify abundances of decapod crustaceans and fishes. This method employs a large cylindrical sampler (1.8 m dia.), dropped from a boom affixed to a small boat, to entrap animals in a 2.6 m² area. Once in place, large fauna are removed with dip nets while water is pumped from the sampler into a 1 mm sq. mesh plankton net. After the sampler is drained, animals on the bottom are picked up by hand. This method is highly effective for measuring densities of decapod crustaceans and small fishes. It is especially useful in habitats, such as marshes and oyster reefs, where trawls and seines cannot be used. Furthermore, drop trap sampling improves on conventional methods (seines and trawls) by quantifying the densities of animals (individuals/unit area) rather than estimating relative abundances. The technique may be used in water depths of 1 meter or less in marshes, seagrasses, mangroves, oyster reefs, or on bare mud or sand bottoms.

Sets of eight drop-trap samples (covering 2.6 m² apiece) were taken in each of three habitats representing salt marsh, oyster reef and mud bottom. Winter season (December 1988) and summer season (July 1989) conditions were sampled once each. These samples provided the basis for calculating densities of all decapod crustaceans and fishes. Samples were preserved in the field, using 10% Formalin made up with seawater and Rose Bengal stain. In the laboratory, decapod crustaceans and fishes were removed, identified to species, measured and counted. In addition to the drop-trap samples, 10 cm sediment diameter cores (78.5 cm²) were taken within each drop trap to quantify abundances of prey available to larger fauna. The cores were sieved in the field through a 500 micron screen and the remaining material was preserved as described above. In the laboratory, the epifauna and infauna consisting of annelids, peracarids and mollusks were removed, identified and counted. Densities were calculated and served as the basis of our analyses.

Laboratory Procedures

In the laboratory, fishes were counted within 10 mm size intervals (1 to 10, 11 to 20, ...etc.) and decapod crustaceans were counted within 5 mm size intervals (1 to 5, 6 to 10, 11 to 15, ...etc). Infauna and epifauna (annelids, peracarids and mollusks) were identified to species and counted, but not measured for size. All of the data were hand written on forms and then transcribed to microcomputer files using DBase III+. After laboratory processing, faunal samples were stored in 5% Formalin or 70% ETOH to be kept for at least 5 years from the date of collection. All field sheets, laboratory data forms and computer files are to be kept at the NMFS Galveston Laboratory for at least 8 years.

Analytical Procedures

The data were mainly analyzed in a two-way ANOVA with habitat (reef, marsh, bare mud) and season (winter, summer) as factors. Significant interactions were further analyzed to determine relationships between habitat differences and season. Analyses were separately performed on groups of animals, including all fishes, all decapod crustaceans, all annelids, all peracarids (amphipods and tanaids), all penaeids (brown shrimp and white shrimp), game fishes (spotted seatrout, southern flounder, red drum), bait fishes (bay anchovy, pinfish, gulf menhaden, striped mullet), as well as on numerically dominant families and species. Samples from drop-traps and cores were the analytical units using eight replicates of each habitat in each seasonal sample set. The data were log transformed ($\log x + 1$) in ANOVAs to correct for heterogeneity among variances. Probabilities less than 0.05 in test results were considered significant.

Untransformed means and standard errors of faunal densities were tabulated for each species in each habitat during each season. These means are in the Tables 1 through 4. All of the original data were entered in Dbase III+ and are stored on standard 5 1/2 inch magnetic floppy disks.

RESULTS

Fishes and Decapod Crustaceans

During the winter, 10 species of fishes (99 individuals) and 17 species of decapod crustaceans (1,835 individuals) were collected in 24 drop-trap samples (Table 1). Of these, 4 species of fishes were at the reef (89 individuals = 4.3 individuals/m²), 5 species in the salt marsh (6 individuals = 0.3/m²) and 3 species (4 individuals = 0.2/m²) on bare mud. Winter fish abundances, overall, were significantly higher at the reef than either the marsh or bare mud habitats (Fig. 1). But, gobies constituted most of the winter fishes at the oyster reef (Fig. 2) and, accordingly, they were the only winter fish group that was significantly different among habitats. Of decapod crustaceans, 12 species were at the reef (756 individuals = 36/m²), 11 species in the marsh (941 individuals = 45/m²) and 8 species on bare mud (138 individuals = 7/m²) (Table 1). Winter abundances of decapod crustaceans were not different between reef and marsh, but both habitats had significantly more decapods than bare mud (Fig. 1). Of numerically dominant decapods, grass shrimps (palaemonidae) were significantly more abundant in the marsh, and mud crabs (xanthidae) and porcelain crabs (porcellanidae) were significantly more abundant at the reef (Fig. 3).

During the summer season, 23 species of fishes (946 individuals) and 15 species of decapod crustaceans (4,534 individuals) were collected in 24 drop-trap samples (Table 2). Of these, 14 species of fishes were at the reef (702 individuals = 34/m²), 9 species in the salt marsh (206 individuals = 10/m²) and 8 species on bare mud (37 individuals = 1.8/m²) (Table 2). Summer fish abundances, were significantly higher at the oyster reef (like winter abundances, dominated by gobies) than the salt marsh or bare mud habitats. Salt marsh summer fish abundances were significantly higher than on bare mud, and two fish species (pinfish, *Lagodon rhomboides*, and spotted seatrout, *Cynoscion nebulosus*) were significantly more abundant in the salt marsh than at either the reef or mud habitats. Of summer decapod crusta-

Table 1. Winter densities of fishes and decapod crustaceans (2.6 m² drop trap samples) at salt marsh, bare mud (nonvegetated) and oyster reef habitats in West Bay, Texas (December, 1988). + indicates presence and - indicates absence.

West Bay and Confederate Reef Macrofauna/2.6 m sq. (n = 8) December 13-15, 1988	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
SPECIES	Mean	S.E.	Mean	S.E.	Mean	S.E.
FISHES						
<i>Gobiosoma boscii</i>	0.1	0.13	0	0	8.3	2.43
<i>Gobiesox strumosus</i>	0	0	0	0	1.8	0.41
<i>Fundulus grandis</i>	0.3	0.25	0	0	0	0
<i>Symphurus plagiusa</i>	0	0	0.3	0.16	0	0
<i>Lagodon rhomboides</i>	0.1	0.13	0.1	0.13	0	0
<i>Chasmodes bosquianus</i>	0	0	0	0	0.1	0.13
<i>Cynoscion nebulosus</i>	0.1	0.13	0	0	0	0
<i>Fundulus pulvereus</i>	0.1	0.13	0	0	0	0
<i>Gobionellus boleosoma</i>	0	0	0.1	0.13	0	0
<i>Prionotus tribulus</i>	0	0	0	0	0.1	0.13
Cyprinodontidae	0.4	0.26	0	0	0	0
Gobiidae	0.1	0.13	0.1	0.13	8.3	2.43
Sciaenidae	0.1	0.13	0	0	0	0
Bait Fishes	0.1	0.13	0.1	0.13	0	0
Commercial/Sports Fishes	0.1	0.13	0	0	0	0
TOTALS	0.8	0.31	0.5	0.27	11.1	2.52
DECAPOD CRUSTACEANS						
<i>Palaemonetes pugio</i>	106.8	30	2.8	0.86	1.8	0.62
<i>Petrolisthes armatus</i>	0.9	0.44	0.1	0.13	41.1	9.28
<i>Panopeus herbstii</i>	0.1	0.13	0	0	27.8	3.95
<i>Callinectes sapidus</i>	3.8	1.24	7.4	0.91	0.4	0.26
<i>Eurypanopeus depressus</i>	0	0	0	0	10	1.56
<i>Clibanarius vittatus</i>	0.3	0.16	1.1	1.13	5.5	4.8
<i>Penaeus aztecus</i>	1.4	0.63	5.3	2.08	0	0
<i>Alpheus heterochaelis</i>	1.3	1	0.1	0.13	3.1	1.08
<i>Palaemonetes vulgaris</i>	2.8	1.84	0	0	0.8	0.37
<i>Menippe mercenaria</i>	0	0	0	0	3	0.85
Unknown <i>Palaemonetes</i>	0	0	0	0	0.9	0.4
<i>Penaeus setiferus</i>	0.1	0.13	0.5	0.27	0	0
<i>Libinia dubia</i>	0.3	0.25	0	0	0	0
<i>Pagurus pollicaris</i>	0	0	0	0	0.1	0.13
<i>Penaeus duorarum</i>	0	0	0	0	0.1	0.13
<i>Pinnixa cristata</i>	0	0	0.1	0.13	0	0
<i>Uca spp.</i>	0.1	0.13	0	0	0	0
Grass Shrimp	109.5	30.03	2.8	0.86	2.5	0.78
Penaeid Shrimp	1.5	0.73	5.8	2.16	0.1	0.13
TOTALS	117.6	30.27	17.3	3.53	94.5	11.06
MOLLUSKS						
<i>Mulinia lateralis</i>	+		+		-	
<i>Semele proficua</i>	-		-		+	
<i>Crepidula plana</i>	+		-		+	
<i>Lyonsia hyalina</i>	-		+		-	
<i>Littorina irrorata</i>	+		-		-	
<i>Amygdalum papyrium</i>	+		+		-	
<i>Cyrtopleura costata</i>	+		-		-	
<i>Laevicardium mortoni</i>	-		+		-	
<i>Pyrgocythara plicosa</i>	-		+		-	

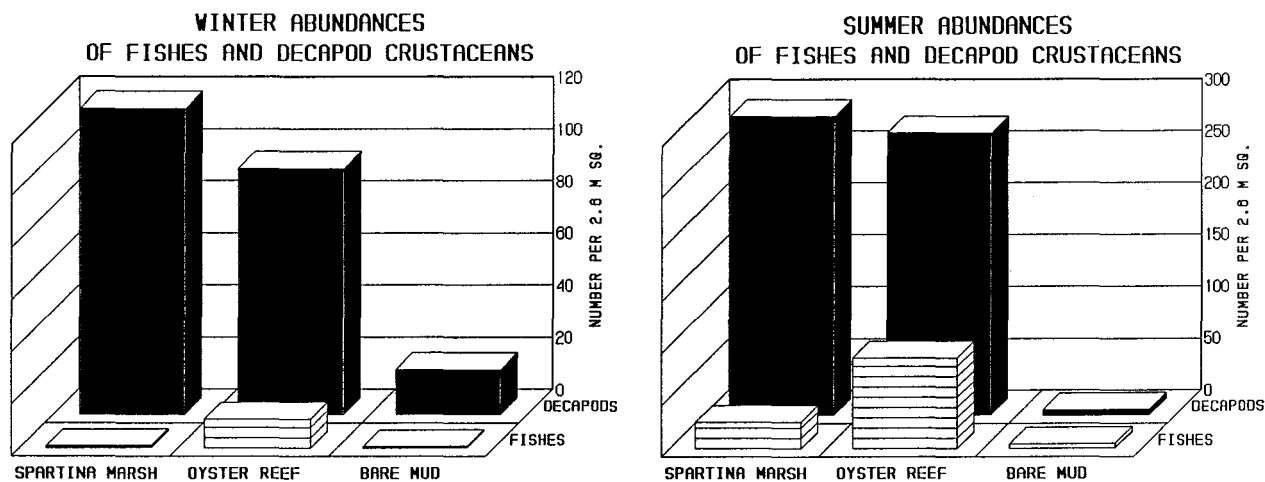


FIGURE 1. Abundances of fishes and decapod crustaceans in salt marsh, oyster reef and bare mud habitats in West Bay, Texas, during December 1988 and July, 1989.

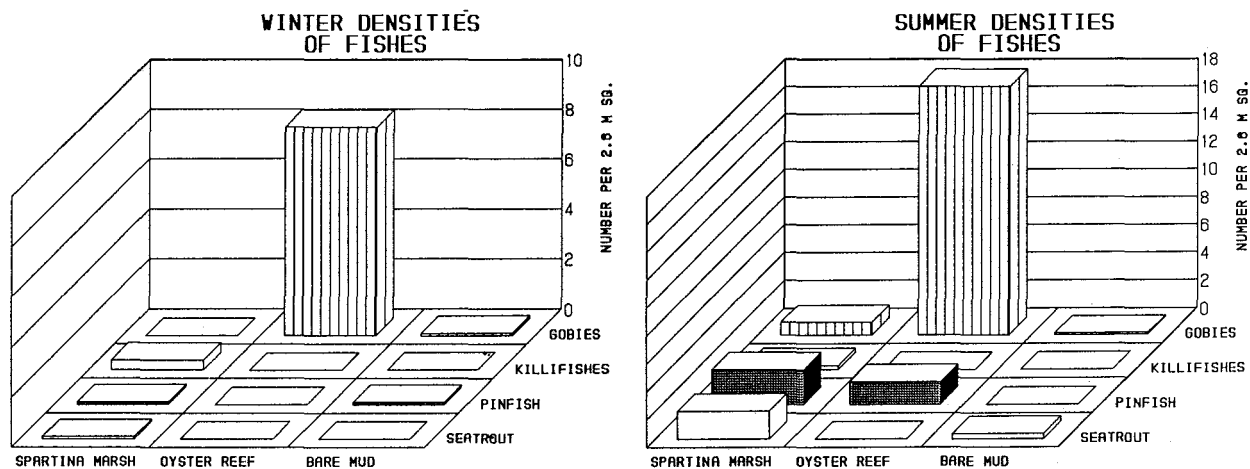


FIGURE 2. Abundances among predominant fishes in salt marsh, oyster reef and bare mud habitats in West Bay, Texas, during December 1988 and July 1989.

TABLE 2. Summer densities of fishes and decapod crustaceans (2.6m² drop trap samples) at salt marsh, bare mud (nonvegetated) and oyster reef habitats taken in West Bay, Texas (July, 1989).

West Bay and Confederate Reef Macrofauna/2.6 m sq. (n = 8) July 14, 21, 25, 1989	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
SPECIES						
FISHES						
<i>Anchoa mitchilli</i>	0	0	2.5	1.22	43.8	42.33
<i>Menidia beryllina</i>	18.9	9.62	0.1	0.13	4.1	3.98
<i>Gobiosoma boscii</i>	0.9	0.74	0.1	0.13	17.5	2.96
<i>Gobiesox strumosus</i>	0	0	0	0	16.1	4.22
<i>Lagodon rhomboides</i>	2.5	0.5	0	0	1.6	0.5
<i>Cynoscion nebulosus</i>	2	0.5	0.4	0.38	0	0
<i>Pomatomus saltatrix</i>	0	0	0	0	1.1	0.67
<i>Chasmodes bosquianus</i>	0	0	0	0	0.9	0.3
<i>Lepomis cyanella</i>	0	0	0	0	0.9	0.61
<i>Symphurus plagiatus</i>	0	0	0.8	0.25	0	0
<i>Brevoortia patronus</i>	0	0	0.3	0.25	0.3	0.25
<i>Syngnathus scovelli</i>	0.6	0.26	0	0	0	0
<i>Opsanus beta</i>	0	0	0	0	0.5	0.38
<i>Hypsoblennius ionthas</i>	0	0	0	0	0.4	0.38
<i>Mugil cephalus</i>	0	0	0	0	0.4	0.38
<i>Paralichthys lethostigma</i>	0.4	0.18	0	0	0	0
<i>Fundulus grandis</i>	0.3	0.25	0	0	0	0
<i>Leiostomus xanthurus</i>	0	0	0.3	0.16	0	0
<i>Achirus lineatus</i>	0.1	0.13	0	0	0	0
<i>Archosargus probatocephalus</i>	0	0	0	0	0.1	0.13
<i>Bairdiella chrysoura</i>	0.1	0.13	0	0	0	0
<i>Eucinostomus argenteus</i>	0	0	0.1	0.13	0	0
<i>Myrophis punctatus</i>	0	0	0	0	0.1	0.13
Unknown fish species	0	0	0.1	0.13	0	0
Cyprinodontidae	0.3	0.25	0	0	0	0
Gobiidae	0.9	0.74	0.1	0.13	17.5	2.96
Sciaenidae	2.1	0.48	0.6	0.38	0	0
Bait Fishes	2.5	0.5	2.5	1.22	45.8	42.48
Commercial/Sports Fishes	2.4	0.53	0.4	0.38	0	0
TOTALS	25.8	9.58	4.6	1.13	87.8	43.97
DECAPOD CRUSTACEANS						
<i>Palaemonetes pugio</i>	221.5	31.25	0.1	0.13	0.8	0.41
<i>Panopeus herbstii</i>	0.4	0.26	0.1	0.13	100.1	14.9
<i>Petrolisthes armatus</i>	0	0	0	0	87.5	24.66
<i>Eurypanopeus depressus</i>	0	0	0.1	0.13	60.6	13.36
<i>Penaeus aztecus</i>	25	3.47	2.8	1.19	0	0
<i>Callinectes sapidus</i>	21.5	4.41	1.1	0.44	0.8	0.25
<i>Alpheus heterochaelis</i>	1.3	0.65	0.1	0.13	15	5.07
<i>Penaeus setiferus</i>	11	3.43	0.9	0.52	0	0
<i>Menippe mercenaria</i>	0.3	0.25	0.1	0.13	6.8	1.21
<i>Clibanarius vittatus</i>	3.6	2.15	0	0	0.8	0.49
<i>Palaemonetes intermedius</i>	1.8	1.75	0	0	0	0
<i>Palaemonetes vulgaris</i>	1.5	0.98	0	0	0	0
<i>Uca longisignalis</i>	0.5	0.38	0	0	0	0
<i>Penaeus duorarum</i>	0.3	0.25	0.1	0.13	0	0
Xanthidae, unknown species	0	0	0	0	0.4	0.38
<i>Neopanope texana</i>	0.1	0.13	0	0	0	0
Unknown <i>Palaemonetes</i>	0	0	0.1	0.13	0	0
Grass Shrimp	224.8	32.06	0.3	0.16	0.8	0.41
Penaeid Shrimp	36.3	6.4	3.8	1.11	0	0
TOTALS	288.6	29.82	5.6	1.53	272.6	48.83

TABLE 2. (continued): + indicates presence and - indicates absence.

West Bay and Confederate Reef Macrofauna/2.6 m sq. (n = 8) July 14, 21, 25, 1989	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
SPECIES						
MOLLUSCA						
<i>Mulinia lateralis</i>	-		+		-	
<i>Littorina irrorata</i>	+		+		-	
<i>Rangia cuneata</i>	-		+		+	
<i>Enis spp. (Minor)</i>	+		+		-	
<i>Cerithidea pliculosa</i>	+		+		-	
<i>Crassostrea virginica</i>	-		-		+	
<i>Crepidula plana</i>	+		-		+	
<i>Amygdalum papyrium</i>	+		+		-	
<i>Nassarius vibex</i>	-		-		+	
<i>Pyrgocythara plicosa</i>	-		-		+	
<i>Tagelus spp.</i>	+		-		-	
Unknown molluscan species	+		-		-	

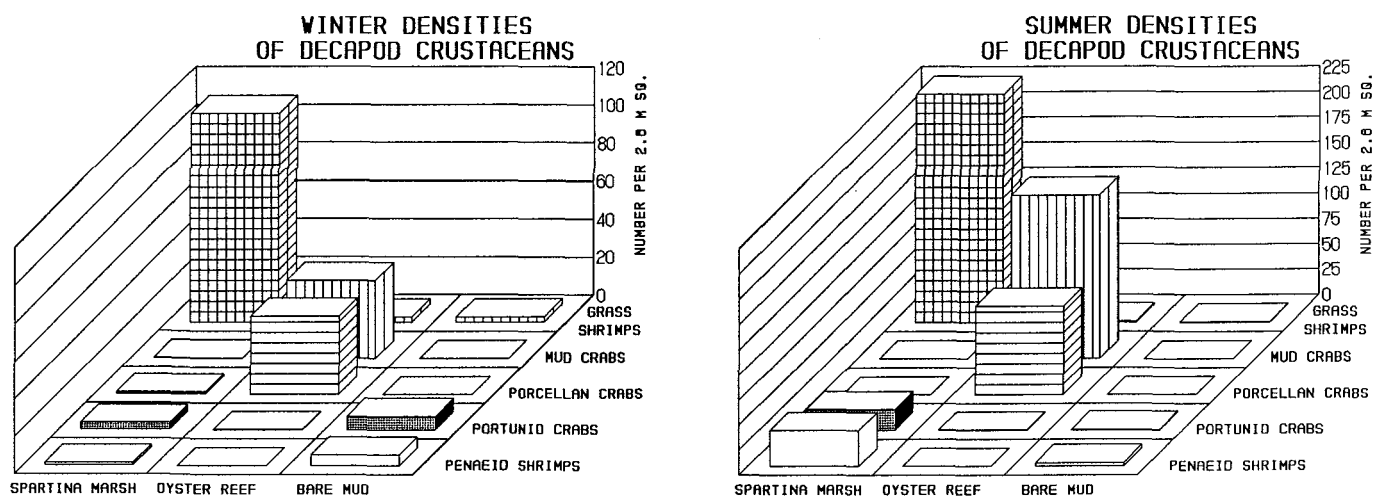


FIGURE 3. Abundances among predominant decapod crustaceans in salt marsh, oyster reef and bare mud habitats in West Bay, Texas during December 1988 and July 1989.

ceans 8 species were at the reef (2,181 individuals = 105/m²), 13 species in the marsh (2,309 individuals = 111/m²), and 9 species in bare mud habitat (45 individuals = 2.2/m²) (Table 2).

Including both seasons, overall fish abundances differed significantly between seasons (summer > winter) and among habitats (reef > marsh > mud). However, the naked goby, *Gobiosoma bosci*, was the only fish significantly more abundant on the oyster reef in both seasons; other numerically dominant reef fishes including skillet fish, *Gobiesox strumosus*, and bay anchovy, *Anchoa mitchilli*, had season*habitat interactions due to low winter densities. Similarly, abundant fishes in the salt marsh, including pinfish and inshore silverside, *Menidia beryllina*, had low winter numbers and significant season*habitat interaction. Nonetheless, the Gulf killifish, *Fundulus grandis*, though low in density, occurred only in salt marsh habitat, both during the winter and the summer. Abundances of decapod crustaceans also exhibited significant season*habitat interaction. Several mud crabs, *Eurypanopeus depressus* and *Panopeus herbstii*, and the porcelain crab, *Petrolisthes armatus*, were most abundant on the reef, and the grass shrimp, *Palaemonetes pugio* was most abundant in the marsh, but each had season*habitat interaction.

Economically Important Species

The game fishes spotted seatrout and southern flounder (*Paralichthys lethostigma*) and valued bait fishes, pinfish and killifish, were mostly, if not entirely, in marsh habitat (Tables 1 and 2; Fig. 2). Likewise, abundances of brown shrimp (*Penaeus aztecus*), white shrimp (*Penaeus setiferus*), and blue crab (*Callinectes sapidus*) were higher in the marsh than the other habitats (Tables 1 and 2; Fig. 3). However, winter abundances of these species were so low that each had significant season*habitat interaction. Within the summer season, all except southern flounder were significantly more abundant in marsh habitat than either oyster reef or mud bottom. The only economically important species without season*habitat interaction was the stone crab (*Menippe adina*; according

to Williams and Felder 1986), which was significantly more abundant at the reef than in other habitats.

Infauna and Epifauna

Infauna and epifauna, potentially available as foods for fishes and decapod crustaceans, differed in abundances among habitats but not between winter and summer seasons. These forage species were comprised of annelid worms (first ranked in abundance), peracarid crustaceans (second ranked in abundance) and mollusks (a distant third ranked in abundance) (Tables 3 and 4; Fig. 4). Abundances of annelids differed significantly between highest numbers on the oyster reef and lowest numbers on mud bottom, but salt marsh abundances did not differ from either reef or mud habitat. Peracarid abundances followed the same pattern as annelids (oyster reef highest, marsh intermediate and mud lowest) except that all habitats differed significantly. Among annelid species, the capitellid *Mediomastus californiensis* was most abundant on the reef (77%) and the spionid *Streblospio benedicti* was most abundant in the marsh (77%) and on mud bottom (87%) (Tables 3 and 4). *Mediomastus* densities were significantly greater on the reef than in marsh or mud habitats (marsh and mud did not differ) during winter and summer seasons. By contrast, *Streblospio* densities were significantly greater in marsh and mud habitats than on the reef (again, marsh and mud did not differ). Among peracarids, the tanaid *Hargeria rapax* was most abundant in the marsh (Tables 3 and 4). But, *Hargeria* densities did not differ between the marsh and reef, nor between seasons, and densities of both habitats differed significantly from mud bottom. The amphipods *Elasmopus levis* and *Melita nitida* were the most abundant peracarids at the oyster reef, and significantly more abundant on the reef than in the marsh or on bare mud (Tables 3 and 4). Their abundances did not differ seasonally. On mud bottom, the amphipods *Ampelisca abdita* and *Corophium* spp. were numerically dominant (Tables 3 and 4). However, only *Ampelisca* was significantly more dense on mud bottom than either

TABLE 3. Winter densities of forage animals (78.5 cm²) in salt marsh, bare mud (nonvegetated) and oyster reef habitats in West Bay, Texas (December, 1988).

West Bay and Confederate Reef Benthos/78.5 cm sq. (n=8) December 13-15, 1988	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
ANNELEDIDS						
<i>Mediomastus californiensis</i>	5.9	4.13	0.6	0.5	242.8	35.91
<i>Streblospio benedicti</i>	147.5	79.54	69.3	23.94	0	0
<i>Nereis falsa</i>	0.5	0.5	0	0	18.4	6.32
<i>Oligochaete, unidentified</i>	5.4	2.88	7	3.07	1.5	0.53
<i>Capitella capitata</i>	4.3	1.85	2.3	1.37	0.3	0.25
<i>Heteromastis filiformis</i>	3.6	1.56	3.3	1.31	0	0
<i>Boccardia hamata</i>	0	0	0	0	6.1	3.23
<i>Hydroides dianthus</i>	0	0	0	0	5.5	2
<i>Syllis (Typosyllis) cf. lutea</i>	0	0	0	0	5.5	2.12
<i>Nereis (Neanthes) succinea</i>	0.1	0.13	0	0	5.1	1.25
<i>Brania cf. clavata</i>	0.3	0.25	0	0	4.8	1.47
<i>Nereis pelagica</i>	0	0	0	0	4.8	1.68
<i>Gyptis cf. brevipalpa</i>	0	0	0	0	3.8	0.9
<i>Schistomeringos cf. pectinata</i>	0.1	0.13	0	0	3.1	0.91
<i>Mediomastus ambiseta</i>	0.5	0.5	2.1	1.11	0	0
<i>Nereis spp.</i>	0	0	0	0	2.3	2.25
<i>Marphysa sanguinea</i>	0	0	0	0	2.1	0.74
<i>Boccardiella ligerica</i>	0	0	0	0	1.5	0.82
<i>Nereiphylla fragilis</i>	0	0	0	0	1.5	0.53
<i>Eumida sanguinea</i>	0	0	0	0	1.4	0.46
<i>Laeonereis culveri</i>	0	0	0.4	0.18	0.9	0.88
<i>Proceraea cornuta</i>	0	0	0	0	1	0.46
<i>Polydora websteri</i>	0	0	0	0	0.9	0.48
<i>Pista palmata</i>	0	0	0	0	0.8	0.41
<i>Hobsonia gunneri</i>	0	0	0.4	0.18	0.3	0.25
<i>Polydora ligni</i>	0.3	0.25	0	0	0.3	0.16
<i>Tharyx annulosus</i>	0	0	0	0	0.5	0.38
<i>Aricidea (Aricidea) wassi</i>	0	0	0	0	0.4	0.26
<i>Enoplobranchus cf. sanguineus</i>	0	0	0	0	0.4	0.18
<i>Sabella microphthalmia</i>	0	0	0	0	0.3	0.16
<i>Syllis (Typosyllis) sp. D</i>	0	0	0	0	0.3	0.16
<i>Tharyx marioni</i>	0	0	0	0	0.3	0.16
<i>Aricidea (Acmira) philbinae</i>	0	0	0.1	0.13	0	0
<i>Ceratonereis irritabilis</i>	0.1	0.13	0	0	0	0
<i>Dialychone spp.</i>	0	0	0	0	0.1	0.13
<i>Eumida spp.</i>	0	0	0	0	0.1	0.13
<i>Lysidice ninetta</i>	0.1	0.13	0	0	0	0
<i>Maldanid sp.</i>	0	0	0.1	0.13	0	0
<i>Megaloma spp.</i>	0	0	0	0	0.1	0.13
<i>Paleanotus heteroseta</i>	0	0	0	0	0.1	0.13
<i>Scoloplos fragilis</i>	0	0	0	0	0.1	0.13
<i>Spiophanes missionensis</i>	0.1	0.13	0	0	0	0
<i>Stenionereis martini</i>	0	0	0	0	0.1	0.13
<i>Tharyx sp.</i>	0	0	0.1	0.13	0	0
<i>Unknown annelid A</i>	0	0	0	0	0.1	0.13
TOTALS	168.8	88.39	85.6	24.86	317.1	46.21

TABLE 3. (continued).

West Bay and Confederate Reef Benthos/78.5 cm sq. (n=8) December 13-15, 1988	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
SPECIES						
PERACARID CRUSTACEANS						
<i>Hargeria rapax</i>	47.1	30.92	0.8	0.37	16.8	10.98
<i>Elasmopus cf. levis</i>	0	0	0	0	47.1	9.63
<i>Corophium spp.</i>	11.5	6.48	5.9	2.75	6.3	5.27
<i>Melita cf. nitida</i>	0	0	0	0	9	2.33
<i>Grandidierella bonneroides</i>	0.1	0.13	0	0	7.1	2.64
<i>Ampelisca abdita</i>	0.3	0.25	4.9	1.77	0	0
<i>Caprella cf. equilibria</i>	0.3	0.25	0	0	2.4	1.18
<i>Cassinidea ovalis</i>	0	0	0	0	2.5	1.31
<i>Mysidae, unknown species</i>	1.5	1.24	0	0	0	0
<i>Gammarus mucronatus</i>	0.3	0.25	0.5	0.19	0.1	0.13
<i>Panopeus herbstii</i>	0	0	0	0	0.9	0.35
<i>Amphilocheus sp. B</i>	0	0	0	0	0.8	0.37
<i>Petrolisthes armatus</i>	0	0	0	0	0.6	0.38
<i>Edotea montosa</i>	0	0	0.5	0.5	0	0
<i>Balanus spp.</i>	0	0	0	0	0.1	0.13
<i>Callinectes sapidus</i>	0	0	0.1	0.13	0	0
<i>Cumacean, unidentified</i>	0	0	0.1	0.13	0	0
<i>Palaemonetes pugio</i>	0.1	0.13	0	0	0	0
<i>Pontogeneiidae spp.</i>	0	0	0	0	0.1	0.13
<i>Sesarma reticulatum</i>	0.1	0.13	0	0	0	0
TOTALS	61.3	36.44	12.8	4.56	93.8	20.64
MOLLUSCA						
<i>Diplothyra smithii</i>	0	0	0	0	1.4	0.71
<i>Semele proficua</i>	0	0	0	0	1.1	0.52
<i>Crepidula plana</i>	0	0	0	0	1	0.38
<i>Sphenia antillensis</i>	0	0	0	0	0.8	0.37
<i>Odostomia impressa</i>	0	0	0	0	0.6	0.63
<i>Tagelus spp.</i>	0.4	0.38	0.1	0.13	0	0
<i>Acteocina canaliculata</i>	0	0	0.3	0.25	0	0
<i>Crassostrea virginica</i>	0	0	0	0	0.3	0.16
<i>Anachis obesa</i>	0	0	0	0	0.1	0.13
<i>Caecum pulchellum</i>	0	0	0	0	0.1	0.13
<i>Cerithidea pliculosa</i>	0.1	0.13	0	0	0	0
<i>Eulimastoma sp.</i>	0.1	0.13	0	0	0	0
<i>Nudibranch spp.</i>	0	0	0	0	0.1	0.13
<i>Tellina spp.</i>	0	0	0.1	0.13	0	0
<i>Turbonilla cf. portoricana</i>	0	0	0	0	0.1	0.13
Unknown molluscan species	0.1	0.13	0	0	0	0
TOTALS	0.8	0.49	0.5	0.5	5.6	2.4
OTHERS						
Anemone	1.8	1.49	0	0	25	9.19
Nemertean (unknown species)	0.1	0.13	0	0	0.5	0.27
Unknown invertebrate	0	0	0	0	0.3	0.16
Dipteran Larva B	0	0	0	0	0.1	0.13
TOTALS	1.9	1.61	0	0	25.9	9.07

TABLE 4. Summer densities of forage animals (78.5 cm²) in salt marsh, bare mud (nonvegetated) and oyster reef habitats in West Bay, Texas (July, 1988).

West Bay and Confederate Reef Benthos/78.5 cm sq. (n=8) July 14, 21, 25, 1989	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
SPECIES						
ANNELIDS						
<i>Streblospio benedicti</i>	127.9	20.95	91.4	13.58	1.1	0.61
<i>Mediomastus californiensis</i>	0.3	0.16	1	0.53	116.9	14.85
<i>Oligochaete, unidentified</i>	33	21.42	1.9	1.22	0.6	0.26
<i>Capitella capitata</i>	12.6	3.29	1.3	0.56	0	0
<i>Brania cf. clavata</i>	0	0	0.1	0.13	8.1	2.73
<i>Euchone spp.</i>	7.1	7.13	0	0	0	0
<i>Nereis (Neanthes) succinea</i>	0.8	0.53	0.3	0.25	3.1	1.25
<i>Eumida sanguinea</i>	0	0	0	0	3.8	1.11
<i>Marphysa sanguinea</i>	0.3	0.25	0	0	1.9	0.52
<i>Heteromastis filiformis</i>	1.3	0.75	0.8	0.37	0	0
<i>Nereis falsa</i>	0	0	0	0	2.1	0.77
<i>Gyptis cf. brevipalpa</i>	0.1	0.13	0	0	1.5	0.73
<i>Hobsonia gunneri</i>	0.6	0.32	1	0.63	0	0
<i>Pista palmata</i>	0	0	0	0	1.5	0.89
<i>Nereiphylla fragilis</i>	0	0	0	0	1	0.87
<i>Sphaerosyllis taylori</i>	0	0	0	0	0.9	0.58
<i>Hydroides protulicola</i>	0	0	0	0	0.8	0.75
<i>Podarke sp. A.</i>	0	0	0	0	0.8	0.31
<i>Polydora ligni</i>	0.1	0.13	0	0	0.6	0.38
<i>Boccardiella cf. sp. A</i>	0	0	0	0	0.6	0.32
<i>Cirrophorus sp.</i>	0	0	0	0	0.6	0.5
<i>Laeonereis culveri</i>	0.5	0.5	0.1	0.13	0	0
<i>Pomatoceros americanus</i>	0	0	0	0	0.6	0.32
<i>Ceratonereis irritabilis</i>	0	0	0	0	0.5	0.27
<i>Proceraea cornuta</i>	0	0	0	0	0.5	0.27
<i>Schistomeringos cf. pectinata</i>	0	0	0	0	0.5	0.19
<i>Aricidea (Acmira) philbinae</i>	0	0	0.4	0.38	0	0
<i>Euclymene sp.</i>	0	0	0.4	0.18	0	0
<i>Mediomastus spp.</i>	0	0	0.3	0.25	0	0
<i>Tharyx sp.</i>	0	0	0	0	0.3	0.25
<i>Glycera americana</i>	0	0	0.1	0.13	0.1	0.13
<i>Drilonereis longa</i>	0	0	0	0	0.1	0.13
<i>Lumbrineris verrilli</i>	0	0	0	0	0.1	0.13
<i>Melinna maculata</i>	0	0	0.1	0.13	0	0
<i>Nereis pelagica</i>	0.1	0.13	0	0	0	0
<i>Stenonereis martini</i>	0	0	0.1	0.13	0	0
<i>Syllidae, unknown</i>	0	0	0	0	0.1	0.13
<i>Syllidae (syllinae?)</i>	0	0	0	0	0.1	0.13
<i>Tharyx marioni</i>	0	0	0	0	0.1	0.13
TOTALS	184.6	31.47	99.1	14.22	149	13.88

TABLE 4. (continued).

West Bay and Confederate Reef Benthos/78.5 cm sq. (n=8) July 14, 21, 25, 1989	HABITAT TYPE					
	<i>Spartina</i>		Non-vegetated		Oyster Reef	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
SPECIES						
PERACARID CRUSTACEANS						
<i>Hargeria rapax</i>	30.1	17.34	0.3	0.16	16.5	4.94
<i>Elasmopus cf. levis</i>	0	0	0	0	33.6	11
<i>Melita cf. nitida</i>	0	0	0	0	23.5	10.72
<i>Cassinidea ovalis</i>	0	0	0	0	5.1	1.74
<i>Melita spp.</i>	0	0	0	0	4.9	3.49
<i>Grandierella bonneroides</i>	0.3	0.25	0	0	4.5	1.7
<i>Corophium spp.</i>	0.5	0.38	0	0	3.9	1.48
<i>Ampelisca abdita</i>	0	0	2.9	0.83	0.1	0.13
<i>Eurypanopeus depressus</i>	0	0	0	0	1.9	0.64
<i>Mysidae, unknown species</i>	0.1	0.13	0.6	0.26	0.8	0.62
<i>Panopeus herbstii</i>	0	0	0	0	1.3	0.31
<i>Petrolisthes galathinus</i>	0	0	0	0	1.3	0.41
<i>Mysidae, unknown</i>	0.1	0.13	0.6	0.63	0	0
<i>Edotea montosa</i>	0.1	0.13	0.1	0.13	0	0
<i>Balanus spp.</i>	0	0	0	0	0.1	0.13
<i>Gammarus mucronatus</i>	0.1	0.13	0	0	0	0
<i>Uca spp.</i>	0.1	0.13	0	0	0	0
TOTALS	31.5	17.95	4.5	0.98	97.4	18.7
MOLLUSCA						
<i>Caecum pulchellum</i>	0	0	0	0	4.8	2.74
<i>Vitrinella floridana</i>	0	0	0	0	4.4	2.38
<i>Odostomia impressa</i>	0	0	0	0	2.3	0.77
<i>Odostomia spp.</i>	0	0	0	0	1.5	1.36
<i>Anachis obesa</i>	0	0	0	0	1.1	0.4
<i>Acteocina canaliculata</i>	0	0	0.3	0.16	0.5	0.5
<i>Epitonium albidum</i>	0	0	0	0	0.8	0.41
<i>Mysella planulata</i>	0	0	0	0	0.6	0.26
<i>Caecum johnsoni</i>	0	0	0	0	0.5	0.5
<i>Semele proficua</i>	0	0	0	0	0.5	0.19
<i>Crepidula plana</i>	0	0	0	0	0.4	0.26
<i>Mulinia lateralis</i>	0	0	0.4	0.38	0	0
<i>Pyrgocythara plicosa</i>	0	0	0	0	0.4	0.26
<i>Diplodonta soror</i>	0	0	0	0	0.3	0.25
<i>Crassinella lunulata</i>	0	0	0	0	0.1	0.13
<i>Enis spp. (Minor)</i>	0	0	0.1	0.13	0	0
<i>Laevicardium mortoni</i>	0	0	0	0	0.1	0.13
<i>Sphenia antillensis</i>	0	0	0	0	0.1	0.13
TOTALS	0	0	0.8	0.49	18.3	6.82
OTHERS						
<i>Anemone</i>	0	0	0	0	2.1	0.91
<i>Nemertean (unknown species)</i>	0.1	0.13	0.3	0.25	1.1	0.44
<i>Nematode, unidentified</i>	0.1	0.13	0	0	0	0
TOTALS	0.3	0.16	0.3	0.25	3.4	0.96

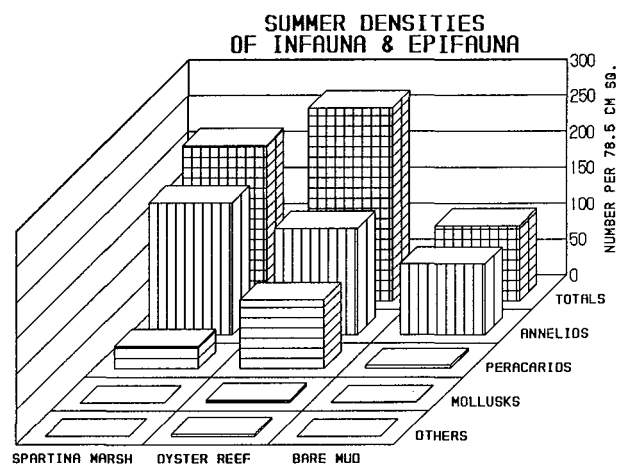
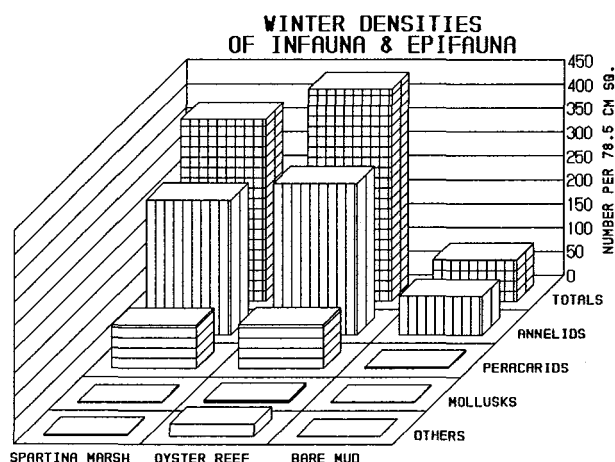


FIGURE 4. Abundances among infauna and epifauna in salt marsh oyster reef and bare mud habitats in West Bay, Texas during December 1988, and July 1989.

marsh or reef, and its densities did not differ seasonally. Mollusks (aside from oysters) were significantly more numerous at the oyster reef than in the marsh or on mud bottom, and seasons were not different (Tables 3 and 4). Other miscellaneous fauna, such as anemones and nemerteans, were generally more common at the oyster reef, but abundances among habitats showed significant season*habitat interaction.

DISCUSSION

Habitat Utilization

The oyster reef was used by similar numbers, but different species of fishes and decapod crustaceans compared to the salt marsh. Infauna and epifauna followed a similar pattern. Reef and marsh habitats were significantly more utilized than bare mud bottom. This demonstrates high attractive value of reef and marsh, but also reveals species differences. Thus, the notion that oyster reef and salt marshes support unique community assemblages is supported, and neither habitat can be viewed as an alternative for the other. An underlying reason for the differences may be due

to differential physical effects of *Spartina* plants and oyster shell. We may hypothesize that, due to differences in substrate characteristics, physical effects alter both the refuge and feeding quality of these habitats for exploiting estuarine species. As a corollary, different infaunal and epifaunal prey develop due to substrate differences. The interactive effect of different physical conditions (such as low mounds of shell versus erect plant stems) and of different forage species (prey) attract different groups of predatory fishes and decapod crustaceans. Indeed, our data show that species of forage animals (annelids and peracarids) are different between the oyster reef and salt marsh. We also show that juveniles of transient predators (penaeid shrimps, blue crab and young game fishes) differ, or are significantly more abundant in the marsh than on the reef. By the latter result, we can infer that additional vertical structure of plants in a marsh provides more refuge for juveniles of game fishes, blue crab (Thomas 1989) and penaeid shrimps (Minello and Zimmerman 1983), or that food to these young predators is more accessible. It is also conceivable that both of these factors work together to greatly magnify the value of marsh for these intermediate size predators. Un-

fortunately, the comparative relationships for a predator of refuge quality, prey accessibility and physical habitat structure between salt marshes and oyster reefs are not known.

Subtidal mud bottom was clearly used by fewer organisms than equivalent areas of marsh or reef. Habitat area and complexity were reduced. Without physical structure, little refuge was available for either the juvenile predators or their prey. Prey or forage species, because of higher predation pressure and less space for habitation, were always kept to low densities. In addition, juveniles of fishery species could only secure refuge by schooling or burrowing. Feeding is unlikely during burrowing; thus, longer searching time required for low density prey, over bottom without cover, increases the risk of being eaten by large predators.

Seasonal Effects

Winter utilization of habitats by economically important species was low, despite the comparatively high abundances of infauna and epifauna available as forage. The only game fish sampled in the winter was a single juvenile spotted seatrout, and it was found in the salt marsh. Juveniles of brown shrimp, blue crab and stone crab also occurred in the winter samples but were more abundant on bare mud than in the marsh or at the reef. Previous investigations by Zimmerman and Minello (1984) and Thomas et al (1990) have shown that both brown shrimp and blue crab are normally more abundant in the marsh than on barren subtidal bottom, in all seasons except the winter. The reason for reversal of habitat preference in the winter is not well explained, but seasonal limitations of habitat availability may be a factor. Seasonal tides are at their lowest during the winter and remain low for longer periods than any other time of the year (Hicks et. al 1983). This renders intertidal salt marsh and oyster reef habitats much less accessible during the winter. As a result, fauna that are attracted to intertidal habitats in the spring, summer and fall cannot exploit them in the winter. However, there are some important exceptions. Juvenile stone crabs were only found

in oyster reef habitat and adults and juveniles apparently occur there year-around (Powell and Gunter 1968; Wilber 1986). Stone crabs feed on oysters (Menzel and Nichy 1958), gastropods and smaller crustaceans (Powell and Gunter 1968). Similarly, grass shrimps and killifishes occur abundantly in the marsh throughout the year and are rare in bare mud and oyster reef habitats (Zimmerman and Minello 1984; and this study).

Summer densities of transient juvenile fishes and decapod crustaceans were significantly greater at the reef and salt marsh than winter densities. By contrast, on mud bottom summer densities were lower than winter densities. Spotted seatrout were among the abundant fishes in the summer, mostly occurring in marsh habitat. The importance of marsh habitat for spotted seatrout is supported by previous work at the site, where juveniles ranging from 8 to 80 mm total length occurred on the marsh surface in abundances about 90% higher than on nonvegetated mud bottom (6years of data, unpublished). These data and our present investigation indicate that salt marsh has substantially more nursery value to spotted seatrout than either oyster reef or mud bottom. Other transient juveniles having significantly higher summer densities in the inundated marsh were brown shrimp, white shrimp and blue crab. These species also indicate that inundated salt marsh is of greater nursery value. Since habitat availability is not complicated by low water levels during the summer, and faunal abundances are higher, summer distributions appear to authentically reflect habitat selection.

CONCLUSIONS

Infauna and epifauna are important foods for juveniles of penaeid shrimps (McTigue and Zimmerman, in review), blue crab (Thomas 1989) and estuarine game fishes (Minello et. al 1988). Since preferred foods attract predators (Pulliam 1974; Bence and Murdoch 1986; Morris 1987), the similarly high abundances of infauna and epifauna in salt marsh and oyster reef habitats should not differ in attraction to decapod crustaceans and fishes. However, this was not the case.

The reef attracted relatively few transient juvenile fishes and even fewer transient decapod crustaceans, while the marsh attracted many. The reasons for density patterns of intermediate size predators apparently extend beyond simple habitat selection related to food abundances. We suspect that the differences resulted from a complex interplay between attraction to foods and predation risk (Holbrook and Schmitt 1988), where, although foods were equally abundant, the predation pressure on transient juveniles was greater on the reef than the marsh. We also propose that foods of these juveniles may be easier to detect and acquire in the salt marsh than on the reef. The visual detection level of prey has been better related to predation pressure than abundance in prey species like amphipods (Luczkovich 1988). Thus, the disproportionate lowering of infauna and epifauna numbers in the marsh in the summer may reflect greater predation pressure on prey, hence greater accessibility. Operating together, better cover and more easily acquired food greatly increases the value of salt marsh habitat, while poor cover and limited food accessibility correspondingly diminishes the habitat value of oyster reef.

Oyster reefs, salt marshes, and bare mud bottoms are also exploited by different associations of estuarine species. In West Bay, Brown (1986) demonstrated that habitat selection differences among demersal copepods were related to substrate differences in sand, mud and oyster reef habitats. Such habitat-related faunal associations may be partly explained by effects of the physical environment on predator-prey interactions. Oyster reefs may afford less protection to intermediate sizes of transient estuarine fauna than marsh vegetation used as structural cover but more than mud bottom which is suitable as burrowing refuge. Foods on mud bottom are also sparse, requiring more time and energy for acquisition. On the reef, food may be abundant but difficult to secure, again necessitating greater time and energy for acquisition. By contrast, food in a salt marsh, especially epifauna, is relatively easy to find and secure. However, such differences between habitats concerning protective and feeding functions are still not well defined nor tested. Addressing the issue

of comparative value of habitat functions should be an essential goal of further estuarine research.

LITERATURE CITED

- Bahr, L. M., Jr. 1974.** Aspects of the structure and function of the intertidal oyster reef community in Georgia. Ph.D. Dissertation. University of Georgia, Athens.
- Bahr, L. M., and W. P. Lanier 1981.** The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-81/15, 105 pages.
- Bence, J. R., and W. W. Murdoch 1986.** Prey size selection by the mosquitofish: relation to optimal diet theory. *Ecology* 67:324-336.
- Brown, E. K. 1986.** Substrate selection by demersal calanoid copepods in shallow waters of Galveston Bay, Texas. M.S. Thesis. Dept. Biology, Texas A&M University, College Station. 77 pages.
- Burrell, V. G., Jr. 1986.** Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Atlantic)—American oyster. U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.57), 17 pages.
- Butler, P. A. 1954.** Summary of our knowledge of the oyster in the Gulf of Mexico. U.S. Fish Wildl. Serv. Bull. 89:479-489.
- Dame, R.F. 1979.** The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. *Proc. Natl. Shellfish Assoc.* 69:6-10.
- Galtsoff, P. S. 1964.** The American oyster *Crassostrea virginica* (Gmelin). U.S. Fish Wildl. Serv. Fish. Bull. 64:1-480.

- Hicks, S. D., H. A. Debaugh Jr. and L. E. Hickman 1983. Sea level variations for the United States 1855-1980. NOAA/NOS Rep., National Ocean Survey, Tides and Water Levels Branch, Rockville, MD. 170 pp.
- Holbrook, S. J. and R. J. Schmitt 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69:125-134.
- Luczkovich, J. P. 1988. The role of prey detection in selection of prey by pinfish *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 123: 15-30.
- McTigue, T. and R. Zimmerman. Carnivory versus herbivory in white shrimp (*Penaeus setiferus*) and brown shrimp (*P. aztecus*) (manuscript in review).
- Menzel, R. W. and F. E. Nichy 1958. Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. *Bull. Mar. Sci.* 8:125-145.
- Minello, T.J. and R.J. Zimmerman 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *J. Exp. Mar. Biol. Ecol.* 72:211-231.
- Minello, T.J., R.J. Zimmerman and T.E. Czapla 1988. The diet of small fishes in Lavaca Bay, Texas, 1985-86. NOAA/NMFS Galveston Laboratory Report to Texas Water Development Board, 15 pages, 5 tables.
- Morris, D. W. 1987. Ecological scale and habitat use. *Ecology* 68:362-369.
- Powell, E. H., Jr. and G. Gunter 1968. Observations of the stone crab *Menippe mercenaria* (Say), in the vicinity of Port Aransas, Texas. *Gulf Res. Rep.* 2:285-299.
- Pulliam, H. R. 1974. On the theory of optimal diets. *Amer. Nat.* 108:59-75.
- Thomas, J.L. 1989. A comparative evaluation of *Halodule wrightii* Aschers, *Spartina alterniflora* Loisel and bare sand as nursery habitats for juvenile *Callinectes sapidus*. M.S. Thesis, Texas A&M University. 119 pages.
- Thomas, J. T., R. J. Zimmerman and T. J. Minello 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bull. Mar. Sci.* 46(1):(TBA).
- Wells, H. W. 1961. The fauna of oyster beds, with special reference to the salinity factor. *Ecol. Monogr.* 31:239-266.
- Wilber, D. H. 1986. The distribution and daily movement of stone crabs (*Menippe mercenaria*) in an intertidal oyster habitat on the northwest coast of Florida. *Mar. Behav. Physiol.* 12:279-291.
- Williams, A. B., and D. L. Felder 1986. Analysis of the stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proc. Biol. Soc. Wash.* 99(3):517-543.
- Zimmerman, R.J. and T.J. Minello 1984. Densities of *Penaeus aztecus*, *P. setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries* 7:421-433.
- Zimmerman, R.J., T.J. Minello and G. Zamora, Jr. 1984. Selection of vegetated habitat by brown shrimp, *Penaeus aztecus*, in a Galveston Bay salt marsh. *Fish. Bull., U.S.* 82:325-336.